Contextual Control Over Conditioned Responding in an Extinction Paradigm

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Four experiments studied contextual control over rats' freezing to conditioned stimuli (CSs) that had been paired with shock and were then extinguished. In Experiment 1, rats were exposed to a CS A–shock and a CS B–shock pairing in Context C. CS A was then extinguished in Context A, and CS B in Context B. Freezing was renewed when each CS was presented in the context where the other CS had been extinguished. In Experiments 2–4, rats were exposed to a CS A–shock pairing in A and a CS B–shock pairing in B. They were then exposed to Context C where one, both, or neither of the CSs were extinguished, or where both CSs continued to be reinforced. On test, the rats froze more to CS A than to CS B in Context A, and more to CS B than to CS A in Context B, but only if the CSs had been extinguished. Thus, after extinction, rats use contexts to regulate retrieval not only of their memory for extinction, but also of their memory for the original conditioning episode.

Behavioral and neural studies of Pavlovian conditioning have increasingly recognized the importance of contexts in regulating learning and memory (e.g., Balsam & Tomie, 1985; Fanselow & Rudy, 1998). This recognition originated in the Rescorla–Wagner (1972) model, which treats the context as an extended conditioned stimulus (CS) that, like any CS, enters into associations with the unconditioned stimulus (US) and thereby modulates the associative strength of a discrete CS. Subsequent developments of this model (Wagner, 1976, 1981) extended its applications to include the formation of context–CS associations. This extension accommodated long-term habituation and latent inhibition produced by CS preexposures, as well as the attenuation of latent inhibition by a context shift between preexposure and conditioning (e.g., Channell & Hall, 1983; Hall & Channell, 1985; Lovibond, Preston, & Mackintosh, 1984). A separate tradition originating in the study of memory (see Bouton, 1993, 1994, and Hall, 1991, for discussion) has adopted a different conception of the role played by contexts in modulating conditioned performance. This tradition views the context as the background in which memories of CS–US associations are formed, and it supposes that these memories are more likely to be retrieved in the context where they were acquired. Thus, this view treats the context as an occasion setter (Holland, 1983) or modulator (Rescorla, 1985)—a set of cues that, in addition to its direct activation

of CS and US memories, acts to retrieve the memory of the relations that existed between the CS and US.

Evidence from "biconditional" switching experiments shows that contexts can serve this occasion-setting function when explicitly required for the solution of a problem (Good, de Hoz, & Morris, 1998; Kimmel & Ray, 1978; Preston, Dickinson, & Mackintosh, 1986). For instance, animals can learn to respond to CS A in Context A and not in Context B (if the CS signals a US in Context A but not in Context B), while they are concurrently learning to respond to CS B in Context B but not in Context A (if that CS signals the US in Context B but not in Context A). However, the evidence as to whether contexts develop this function in the absence of such explicit training has been inconsistent: There are reports that rats respond more to a CS in its conditioning context than in a different context even when the two contexts are equated for their association with the US (Bonardi, Honey, & Hall, 1990; Hall & Honey, 1989, 1990; Honey, Willis, & Hall, 1990); but there are numerous reports in which responding to CSs generalized across contexts without loss (e.g., Bouton & King, 1983; Bouton & Peck, 1989; Grahame, Hallam, Geier, & Miller, 1990; Lovibond et al., 1984).

One of the factors that may determine whether a context comes to signal a CS–US relation is the reinforcement history of that CS. Swartzentruber and Bouton (1992) reported that rats preexposed to a CS in advance of CS–US pairings responded less to that CS when it was tested outside its conditioning context, whereas rats not preexposed to the CS exhibited transfer of conditioned performance from the conditioning context to the other test context. Recently, we have confirmed this finding in a design that equated the contexts for their association with the US (Westbrook, Jones, Bailey, & Harris, 2000). Specifically, we preexposed rats to a context (C) where, for some rats, two CSs (CS A and CS B) were repeatedly presented in isolation, whereas for other rats no CSs were presented. All rats were then exposed to a pairing of CS A with shock in Context A and to a pairing

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of CS B with shock in Context B, before being tested for responding to the CSs either in their respective conditioning contexts (CS A in A, and CS B in B) or in the reversed contexts (CS A in B, and CS B in A). Rats preexposed to the CSs responded more to each CS in its own conditioning context than in the context where the other CS had been conditioned. In contrast, rats that had not been preexposed to the CSs showed equivalent levels of responding to the CSs irrespective of which context they were tested in.

Bouton (1993, 1994) has proposed a theory of memory retrieval that is consistent with these effects of CS preexposure on context specificity of CS–US associations. This theory holds that animals use contextual information to regulate the retrieval of CS memories when the meaning of the CSs has been rendered ambiguous by a mixed history of association with the US. Thus, when an animal is exposed to a CS–US pairing on some occasions, and to the CS alone on other occasions, it acquires two contrasting memories of that CS, and it uses the environmental and temporal contexts where those memories were acquired to distinguish between them. Bouton has suggested that animals contextualize (i.e., conditionalize to a context) the second, but not the first, memory because the CS is only rendered ambiguous during that second experience. This "second memory" view is consistent with many of the results described earlier, in particular, the demonstrations that rats contextualized their memory of a CS–shock association if they had been previously exposed to that CS without the US but not if the CS was novel at the time of its pairing with shock. Further evidence that animals contextualize their second memories about CSs comes from studies of extinction conducted by Bouton and colleagues (Bouton & Bolles, 1979; Bouton & King, 1983; Bouton & Swartzentruber, 1989). For instance, Bouton et al. have reported that animals conditioned to a CS in one context (A) and then extinguished to that CS in a second context (B) show restoration of conditioned performance when tested back in A. Such restoration does not depend on testing rats back in the conditioning context, because recovery from extinction is also observed in animals that have been conditioned and extinguished in A but tested in B (Bouton & Ricker, 1994). According to Bouton (1993, 1994), the context comes to control the extinction memory because that memory is acquired after the CS has been paired with the US.

One implication of the view that animals contextualize the second memory they acquire about a CS is that the conditioning context should not exert any control over retrieval of the CS–US memory in an extinction paradigm because that memory was acquired first. In other words, unlike the previous demonstrations of contextual control over CS–shock memories in a CS preexposure paradigm, contextual control over CS–US memories should not be observed in an extinction paradigm. The present experiments used an extinction paradigm to confirm evidence for context specificity of extinction and to examine contextual control over the original conditioning memory. These experiments used designs that used three distinctive contexts (see Table 1 for a summary of the designs for each experiment). The designs equated the two test contexts for their associa-

Table 1
Summary of Experimental Designs

Group	Conditioning	Extinction	Test
Experiment 1			
Same	C: CS A+ & CS B+	A: CS A & B: CS B	A: CS A
Different	C: CS A+ & CS B+	A: CS A & B: CS B	B: CS A
Experiment 2			
Not ext con	A: CS A+ & B: CS B+	C: —	A: CS A
Not ext incon	A: CS A+ & B: CS B+	C: —	B: CS A
Ext con	A: CS A+ & B: CS B+	C: CS A & CS B	A: CS A
Ext incon	A: CS A+ & B: CS B+	C: CS A & CS B	B: CS A
Experiment 3			
Ext	A: CS A+ & B: CS B+	C: CS A & CS B	A: CS A & CS B
Continuous reinforcement	A: CS A+ & B: CS B+	C: CS A+ & CS B+	A: CS A & CS B
Experiment 4			
Con	A: CS A+ & B: CS B+	C: CS A	A: CS A & B: CS B
Incon	A: CS A+ & B: CS B+	C: CS A	A: CS B & B: CS A

Note. A, B, and C refer to three separate contexts (A and B were counterbalanced); a clicker and white noise were used as conditioned stimuli (CS A and CS B, counterbalanced); and + denotes pairing of the CS with the shock unconditioned stimulus. Dashes represent exposure to the context without the CS. Ext = extinguished; Con = consistent; Incon = inconsistent.

tion with the US and arranged that conditioning and extinction occurred in different contexts. This enabled us to examine contextual control over the extinction memory (Experiment 1) separately from that established over the conditioning memory (Experiments 2, 3, and 4).

Experiment 1

As noted previously, Bouton and colleagues have reported that rats conditioned and extinguished to a CS in one context exhibit renewal of conditioned responding when tested in a different context. This renewal has been observed in a design that equated the two contexts for their conditioning and extinction histories. Specifically, Bouton and Ricker (1994, Experiment 3) exposed rats to two contexts (A and B) in each of which a CS was first paired with a US and then presented in the absence of that US (e.g., CS A in A and CS B in B). Finally, when tested for conditioned responding to CS A, the rats showed more responding in Context B than in A. However, two other studies that also equated the contexts for their conditioning and extinction histories failed to find evidence for renewal, that is, they found that extinction to CS A in Context A transferred to Context B (Grahame et al., 1990; Lovibond et al., 1984). Thus, further investigation of contextual control over extinction using designs that equate the conditioning and extinction histories of the contexts is warranted.

The aim of Experiment 1 was to investigate whether contextual control over extinction is observed in a three context design, which equates the two test contexts for their extinction histories and ensures that neither is associated with conditioning. The experiment used two counterbalanced CSs. Rats were exposed to separate pairings of each CS with shock in Context C before the CSs were extinguished in separate contexts (CS A was extinguished in Context A, CS B in Context B). Rats were then tested with one of the CSs either in the context where it had been extinguished (Group Same) or in the context where the other CS had been extinguished (Group Different). In this design, no CS–US pairings have occurred in either Context A or Context B, and because the actual chambers that constitute these contexts are counterbalanced, they are equated for any excitation that may generalize from Context C. Finally, because CSs are extinguished in both contexts, they are matched for any inhibitory conditioning that might accrue to them. Therefore, this experiment provides evidence for context specificity of extinction if rats in Group Same show less responding on test than rats in Group Different.

Method

Subjects. Sixteen experimentally naïve male Wistar rats (*Rattus norvegicus*; 340–410 g) were obtained from a colony of Specific Pathogen Free rats maintained by the Combined Universities Laboratory Animal Service, at Little Bay, Sydney. Rats were housed in groups of 8 in white opaque plastic boxes (67-cm depth × 40-cm width × 22-cm height) kept in a colony room maintained on natural light–dark cycle, with food and water continuously available in the wire mesh lids.

Apparatus. Three sets of experimental chambers, each located in separate rooms in the laboratory, were used. The first set (Context C) was used for conditioning, and it consisted of four chambers (23-cm depth × 21-cm width × 20-cm height). The walls and lid of these chambers were constructed of clear plastic, and the floor consisted of stainless steel bars, 2 mm in diameter, spaced 13 mm apart (center to center). Unscrambled AC 50-Hz shock from a constant current generator could be delivered to the floor of each chamber, and the current available to each floor was adjusted by reference to an in-line milliampere meter. Each chamber was cleaned with wet paper towel on removal of a rat. The room was illuminated by two white incandescent bulbs located on the ceiling.

Two further sets of chambers served as Context A and Context B in a counterbalanced fashion. The chambers in one set measured 33-cm height × 31-cm length × 26-cm width). The side walls and ceiling were made of aluminum, and the back and front walls were made of clear plastic. The side walls and ceiling were painted white, and the outside back wall was covered by white cardboard. The floor consisted of stainless steel rods, 6 mm in diameter, spaced 15 mm apart, center to center, with a tray containing bedding material below the floor. The chambers were located in separate compartments of a wooden cabinet, whose floor, ceiling, and walls were painted white. The door of each compartment was kept open to permit observation of the rat. One milliliter of a concentrated rose oil (Cara-Mia, Sydney) was sprayed over the bedding material before each session to provide a distinctive odor. The room was illuminated by a white fluorescent tube located on the ceiling.

Each chamber of the second set measured 30-cm height × 30-cm width × 27-cm length. The side walls and ceiling were made of aluminum, and the back and front walls were made of clear plastic. The side walls and ceiling were painted black, and the outside of the back wall was covered by black cardboard. The floor consisted of stainless steel rods, 2 mm in diameter, spaced 10 mm apart, center to center. Below the floor was a tray containing bedding material. The four chambers were placed in separate compartments of a wooden cabinet whose floor, ceiling, and walls were painted black. The door of each compartment was kept open. One milliliter of concentrated banana essence (Rockman, Sydney) was sprayed onto the bedding material before each session to provide a distinctive odor. The room was illuminated with a red fluorescent tube located on the ceiling.

The background noise level in each room was 65 dB. The behavior of each rat was recorded using a camera mounted on the wall, facing the open compartments in each room. The camera was connected to a video recorder and monitor located in another room in the laboratory. This room also contained the equipment that controlled CS and shock presentations.

Two auditory stimuli served as CS A and CS B in a counterbalanced fashion. One CS was a 30-s presentation of a clicker, which consisted of a 72-dB (A: Brüel & Kjaer, Type 2235) 10-Hz spike (rise time < 1 μs, decay time 250 μs). The other CS was a 30-s presentation of 75-dB continuous white noise. Both stimuli were presented from identical loud speakers (160 mm in diameter, wideband width) mounted on the ceiling of each room 1.5 m above the chambers.

Procedure. Rats were handled for 2 min on each of 3 successive days and assigned to two weight-matched groups (*n* = 8) prior to the start of the experiment. On Day 1, rats were transported to the laboratory and placed into the conditioning chambers (Context C), and after 3 min one of the CSs was presented for 30 s. On termination of the CS, a 0.6-mA 0.5-s shock was delivered through the floor of the chamber. Three minutes after the shock, the other CS was presented for 30 s followed by a 0.6-mA 0.5-s shock. One minute after the second shock, each rat was removed from the chamber and returned to its home box. The order in which the CSs were paired with shock was counterbalanced. On Days 2 and 3, both CSs were extinguished, but in different contexts. Thus, on each day, all rats were placed into Context A and Context B for 18 min, 5 hr apart. During these exposures, CS A was presented for 30 s eight times in Context A, and CS B was presented for 30 s eight times in Context B. The CS presentations began 2 min after the rats were first placed in the chamber, and successive presentations were spaced 2 min apart. On Day 2, the rats were exposed to Context A in the morning and Context B in the afternoon, whereas the order was reversed on Day 3. Each rat was scored for freezing during presentations of the CSs on each of the four extinction sessions. On Day 4, the rats were placed into Context A or Context B where CS A was presented four times for 30 s, each presentation spaced 2 min apart. Thus, one group of rats (Group Same) was tested with CS A in the context where it had been extinguished, whereas the other group (Group Different) was tested with CS A in the context where CS B had been extinguished.

Scoring and statistical analyses. Freezing was defined as the absence of all movement, except that related to breathing (Fanselow, 1980). The behavior of each rat was recorded on videotape, and freezing was rated with a time-sampling procedure in which each rat was observed once every 3 s and scored as either freezing or not. The number of occasions on which the rat failed to move (freezing) was expressed as a percentage of the total number of observations. For this and subsequent experiments, the behavior of each rat was rated by the experimenter during the test, and it was rated again from the videotape by an observer naïve to the rats' group designations. There was high degree of agreement between the two observers: The Pearson product–moment correlations between

their ratings were above .95 in each of the experiments. The data collected by the naïve observer were used for analysis. The data from the extinction sessions were analyzed by a multivariate analysis of variance (MANOVA), testing for the difference in freezing between the two groups, for the linear trend across extinction sessions, and for the Group × Trend interaction (O'Brien & Kaiser, 1985). The data from the test were analyzed by an independent samples Students t test that compared freezing among rats in Group Same with rats in Group Different. The error rate (alpha) for both analyses was set at .05.

Results

Across the extinction sessions on Days 2 and 3, freezing to the CSs gradually decreased for both groups. This decrease in fear across each block of four CS presentations is shown in the left panel of Figure 1. There was a significant linear trend for both groups across blocks, $F = 57.62$, $F_{critical}(1, 14) = 4.6$, confirming that freezing decreased across extinction. There was no difference between the two groups in their overall levels of freezing, $F < 1$, or in their linear trends, $F = 1.23$.

On test, there was virtually no freezing to the context prior to onset of the CS in either Group Same ($M = 0.5\%$) or Group Different ($M = 0.7\%$). Rats in both groups froze when the CS was presented. The freezing averaged across test presentations of the CS is shown in the right panel of Figure 1. The important feature of the data is that the rats in Group Same showed significantly less freezing than rats in Group Different, $t = 2.56$, $t_{critical}(14) = 2.15$.
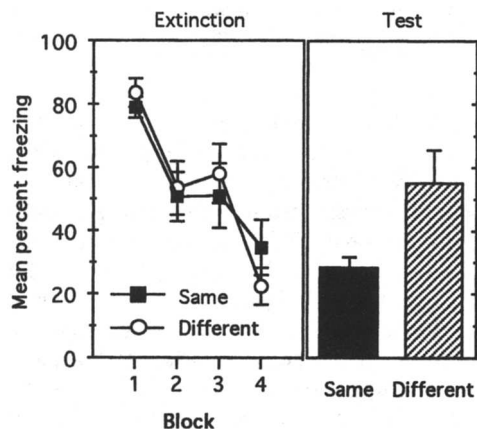
Figure 1. Mean percentage of time spent freezing to the conditioned stimulus (CS) by rats in Experiment 1. Rats were exposed to pairings of two CSs with shock in one context (C), before responding to each CS was extinguished in separate contexts (A and B). The left panel shows the level of freezing to each CS, averaged across blocks of four consecutive presentations, during the extinction sessions. Rats were then tested for freezing to one of the CSs either presented in the context where it had been extinguished (consistent) or in the context where the other CS had been extinguished (inconsistent). The right panel shows the level of freezing for both groups averaged across the four test presentations. Vertical bars represent standard error of the mean.

Discussion

This experiment demonstrated that rats show renewed responding to an extinguished CS if it is presented in a context different from that where it had been extinguished. The rats had not been conditioned in either of the two test contexts, thus neither context was directly associated with the US. Further, because the specific chambers that served as the two contexts were counterbalanced, the contexts were matched for any excitatory conditioning that might generalize to them from the conditioning context. Finally, because CSs were extinguished in both contexts, the two contexts had equal potential to become conditioned inhibitors (see Rescorla, Durlach, & Grau, 1985, for discussion). Thus, the only difference between the two test contexts was that one was associated with extinction of the specific CS that was tested, whereas the other context was associated with extinction of the other CS. The renewal of responding observed when the CS was tested in the inconsistent context cannot be ascribed to any differences between the contexts in their excitatory or inhibitory values. Rather, this renewal demonstrates that extinction of a CS is context specific.

Experiment 2

The demonstration of context specificity of extinction in Experiment 1 is consistent with Bouton's (1993, 1994) proposal that animals use contexts to regulate their retrieval of memories about CSs with a mixed history of reinforcement. According to one version of this proposal, animals contextualize the second memory they acquire about a CS because it is the second memory that renders the CS ambiguous. One important prediction of this view is that rats should not show contextual control over CS–US associations in an extinction paradigm, even though the CS has a mixed history of reinforcement, because the CS–US association is the first memory acquired about the CS. This prediction was tested in the present experiment.

Experiment 2 used a 2 × 2 factorial design. Four groups of rats were exposed to two contexts, which in each context, one of two counterbalanced CSs was paired with a shock US: CS A was paired with shock in Context A, and CS B was paired with shock in Context B. For two groups of rats, responding to both CSs was then extinguished in a third context (C), whereas the other two groups were exposed to Context C, but neither CS was presented. Finally, the rats were tested for responding to CS A in either Context A or B. Thus, Factor 1 was whether the CSs were extinguished or not extinguished, whereas Factor 2 was whether the CS at test was presented in the context where it had been conditioned (Groups Consistent) or in the context where the other CS had been conditioned (Groups Inconsistent).

Method

Subjects and apparatus. Thirty-two experimentally naïve male Wistar rats (*Rattus norvegicus*; 360–450 g) were obtained from the same source and housed in the same manner as in Experiment 1. The three sets of experimental chambers were the same as those used in Experiment 1. The rats were trained in Context A and

Context B. The floors of these chambers were connected to a constant current generator that delivered unscrambled AC 50-Hz shock (the current available to each floor was adjusted by reference to an in-line milliampere meter). The clicker and white noise were used as the two CSs, in a counterbalanced fashion, as in Experiment 1.

Procedure. Rats were handled for 3 days and assigned to four weight-matched groups ($n = 8$). On Day 1, rats were transported to the laboratory and placed into one of the conditioning chambers (Context A or Context B), and after 3 min, CS A was presented for 30 s to rats in Context A, and CS B was presented for 30 s to rats in Context B. On termination of the CS, a single 0.6-mA 0.5-s shock was delivered through the floor of the chamber. After a further minute, each rat was removed and returned to its home box. Five hours later, the rats were placed into the other conditioning chamber (Context B or Context A) where, after 3 min, the other CS was presented for 30 s followed by a single 0.6-mA 0.5-s shock. Thus, the order in which the CSs were conditioned was counterbalanced. For every rat, CS A had been paired with shock in Context A, and CS B had been paired with shock in Context B. On Days 2 and 3, both CSs were extinguished (Ext) for two groups. On each of these days, the Ext rats were placed into Context C twice for 18 min, once in the morning and once in the afternoon (5 hr later). On Day 2, CS A was presented for 30 s eight times during the morning session in Context C; CS B was presented for 30 s eight times during the afternoon session. This order was reversed on Day 3 (i.e., CS B was presented in the morning, and CS A was presented in the afternoon). These CS presentations began 2 min after the rats were first placed in the chamber and were spaced 2 min apart. No shocks were delivered on these days. Across these days, rats in the other two groups (Not Ext) were given equivalent exposures to Context C, but neither of the CSs were presented. On Day 4, the rats were tested. They were placed into Context A or Context B, and CS A was presented four times for 30 s, spaced 2 min apart. Thus, two groups (Groups Ext Consistent and Not Ext Consistent) were tested with CS A in the context where CS A had been conditioned, whereas the other two groups (Ext Inconsistent and Not Ext Inconsistent) were tested with CS A in the context where CS B had been conditioned. To determine whether a ceiling effect may have obscured any difference between the two groups that had not been extinguished, we tested these groups across a further four presentations of the CS. Freezing was scored in the manner described for Experiment 1. The freezing responses to each of the test presentations of the CS were analyzed using a MANOVA (O'Brien & Kaiser, 1985).

Results

The rats in each group showed relatively little freezing to the context in the 30-s period before presentation of the CS on test (means were 6.25% and 7.5% for Groups Ext Consistent and Ext Inconsistent, and 10% and 12.5% for Groups Not Ext Consistent and Not Ext Inconsistent). These differences were not statistically significant, $Fs < 1$.

Freezing during each presentation of the CS on test is presented in Figure 2. It is clear that the levels of freezing displayed by each group were reduced across successive CS presentations. Further, the rats whose fear of the CSs had already been extinguished in Context C showed less freezing than the rats whose fear was not extinguished. The most important feature of this data is that the two extinguished groups differed in their level of freezing. Group Consistent, who were tested in the context where the CS had been
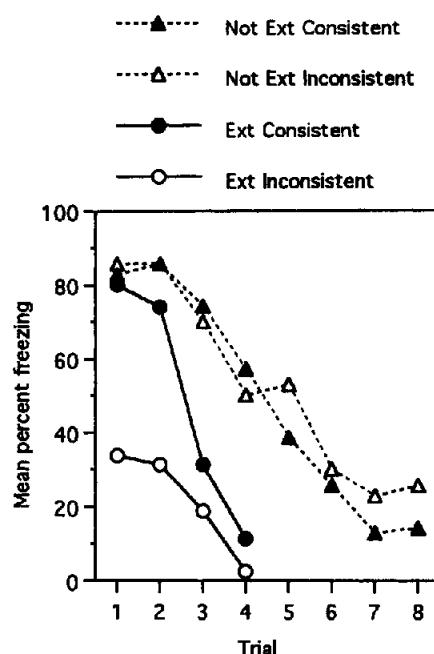

Figure 2. Mean percentage of time spent freezing to the conditioned stimulus (CS) on test by rats in Experiment 2. Rats were exposed to pairing of two CSs with shock in separate contexts (A and B). For two groups (extinguished [Ext]), each CS was presented without the shock in a third context (C). Rats in the other two groups (not extinguished [Not Ext]) were exposed to C, but neither CS was presented. Rats were then tested for freezing to one of the CSs presented either in the context where it had been conditioned (Group Consistent) or in the context where the other CS had been conditioned (Group Inconsistent). Extinguished groups were tested across four presentations of the CS; Nonextinguished groups were tested across eight CS presentations.

conditioned, showed more freezing than Group Inconsistent, who were tested in the context where the other CS had been conditioned. In contrast, there was no such difference between the two groups that had not been extinguished.

The statistical analysis of the data from the first four presentations of the CS confirmed these observations. There were significant main effects for extinction (Groups Ext vs. Non Ext), $F = 34.83$, $F_{critical}(1, 28) = 4.2$, and for context (Groups Consistent vs. Inconsistent), $F = 5.15$, as well as a significant interaction between the two factors, $F = 4.91$. The source of the interaction between extinction and context was identified by pairwise comparisons, which revealed a significant difference between Group Ext Consistent and Group Ext Inconsistent, $F = 10.77$. In contrast, there was no difference between Groups Not Ext Consistent and Not Ext Inconsistent across either the first four presentations or across all eight presentations, $Fs < 1$. There was also a significant linear trend across the initial four CS presentations, $F = 63.79$, showing that freezing extinguished within the test session. This linear trend did not interact with either of the group main effect contrasts, $Fs \leq 3.15$, indicating that the rate of extinction during test was not affected by prior extinction treatment or by the context–CS relation.

Discussion

This experiment has demonstrated that rats show more freezing to a CS when presented in the context where it was paired with a shock US than when the CS was presented in a context where a different CS was paired with shock. However, this context specificity was only observed among rats whose fear of the CS had been extinguished in a third context: There was no evidence for context specificity in the absence of extinction. These findings are consistent with the notion that excitatory memories are contextualized, but only for CSs with a mixed history of reinforcement (Bouton, 1993). Importantly, however, the present findings show that context specificity of a CS–US association can occur even if that association was the first to be learned, at which time the status of the CS–US memory was not ambiguous. Thus, if the CS–US association was the only information learned about that CS, then rats did not show evidence for contextual control over performance of that association. However, if rats were exposed to contradictory information about the CS, specifically, that it was no longer associated with the US, then performance of the original CS–US association was contextually controlled.

Experiment 3

Experiment 2 demonstrated that the conditioning context can come to control rats' retrieval of a CS–US association, but only if the CS has been extinguished. We infer from this demonstration that rats use contextual information to regulate retrieval of their memory for CS–US associations, but only if the status of that association has become ambiguous. However, the design of Experiment 2 confounds the status of the CS–US association (extinguished vs. not extinguished) with the amount of exposure to the CSs and, therefore, the ability to discriminate between them. Specifically, the groups that showed contextual control over responding were exposed 17 times to each CS (once during conditioning and 16 times during extinction), whereas the groups that did not show contextual control were exposed to each CS only once. The increased exposure to the CSs may have established a more detailed representation of those stimuli, thereby enabling Groups Extinguished to discriminate between them (e.g., Honey & Hall, 1989). This perceptual learning afforded by the extra exposure to the CSs may have been sufficient for the extinguished rats to show context specificity of responding to the CSs

Experiment 3 was conducted to test between these alternative explanations for the results of Experiment 2. In this experiment, groups were equated for total exposure to the CSs, but differed in whether the CS–US associations were extinguished or maintained across those exposures. Two groups of rats were exposed to a CS A–shock pairing in Context A and a CS B–shock pairing in Context B. For one group (Ext), both CSs were extinguished in Context C, whereas for the other, Group Continuous Reinforcement (CRF), both CSs were subjected to continuous reinforcement in Context C, whereby each CS presentation was followed by the shock US. In an attempt to ensure that the

level of responding in CRF group was not markedly higher than for the Ext group, the intensity of the shock differed between these conditions. For the Ext group, the shock was set at 0.6 mA for 0.5 s, as before, whereas the shock was reduced to 0.4 mA for 0.5 s for the CRF group. Subsequent to the extinction or continuous reinforcement treatments in Context C, the rats were tested with both CSs in Context A. Thus, each rat was tested with CS A in its conditioning context (consistent) and with CS B in the context where CS A had been conditioned (inconsistent).

Method

Subjects and apparatus. Thirty-two experimentally naïve male Wistar rats (*Rattus norvegicus*; 320–470g) were obtained from the same source and housed in the same manner as in Experiment 1. The three sets of experimental chambers and two CSs described for Experiment 1 were used here.

Procedure. Rats were handled for 3 days and assigned to two weight-matched groups (*n* = 16). On Day 1, rats were transported to the laboratory and placed into one of the conditioning chambers (Context A or Context B), and after 3 min, either CS A (for rats in Context A) or CS B (for rats in Context B) was presented for 30 s. On termination of the CS, all rats received a .5-s shock in which the intensity was either 0.6 mA for those in the Ext group or 0.4 mA for rats in the CRF group. After a further minute, each rat was removed. Five hours later, the rats were placed into the other conditioning chamber (Context B or Context A) where, after 3 min, the other CS was presented for 30 s followed by a shock of the same intensity as before. On Days 2 and 3, for the Ext group, both CSs were extinguished in Context C as in Experiment 2. On these days, the rats in the CRF group were placed into Context C twice a day for 18 min, with the two sessions being separated by 5 hr. During one session, CS A was presented for 30 s eight times, each time followed by a 0.4-mA 0.5-s shock; during the other session, CS B was presented for 30 s eight times, each followed by the 0.4-mA 0.5-s shock. Thus, all groups were given equivalent exposure to the two CSs, but differed in whether the CSs were extinguished or continued to be reinforced across those exposures. On Days 4 and 5, the rats were tested. They were placed into Context A, and one of the CSs was presented four times, each presentation being 30-s and presentations spaced 2-min apart. Half of the rats from each group were tested with the consistent CS (CS A) on Day 4 and with the inconsistent CS (CS B) on Day 5; the remaining rats were tested with CS B on Day 4 and CS A on Day 5. Freezing was scored in the manner described for Experiment 1. The data were analyzed by a MANOVA (O'Brien & Kaiser, 1985), which tested for main effects for group (Ext vs. CRF) and for CS (Consistent vs. Inconsistent). Because test order was counterbalanced within each group, the test order was also entered as a factor in the analysis.

Results

The levels of freezing to the context in the 30-s period prior to the initial test presentation of the CS was low. The means were 5% and 6.7% for Ext rats tested with the Consistent and Inconsistent CSs, and 11.3% and 10.63% for CRF rats tested with the Consistent and Inconsistent CSs. None of the differences among the groups were significant, $F \leq 1.73$. The mean percentage of freezing to each presentation of the consistent and inconsistent CSs on test for both groups is presented in Figure 3. It is clear that the
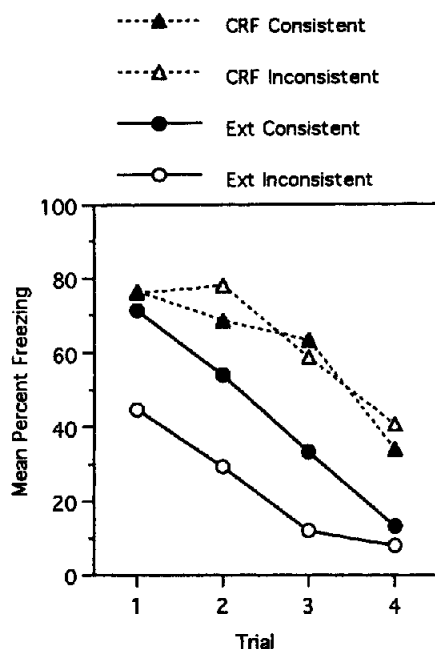
Figure 3. Mean percentage of time spent freezing to the conditioned stimuli (CSs) by rats in Experiment 3. Rats were exposed to pairing of two CSs with shock in separate contexts (A and B). For one group (extinguished [Ext]), each CS was repeatedly presented without the shock in a third context (C). For the other group (continuous reinforcement [CRF]), each CS was repeatedly presented and followed by shock in C. Rats were then tested for freezing across four presentations of each CS, one CS was presented in the context where it had been conditioned (consistent), and the other CS was presented in the context where the first CS had been conditioned (inconsistent).

Ext group showed less freezing than the CRF group. Moreover, the Ext rats were clearly freezing more to the consistent CS than to the inconsistent CS, whereas the CRF rats showed equivalent levels of freezing to each CS. Finally, the level of freezing to each CS appeared to decrease across test presentations for both groups.

The statistical analysis revealed that there was a significant main effect for test order (Test 1 vs. Test 2), $F = 11.85$, $F_{critical}(1, 26) = 4.22$, but this factor did not interact with any other factor, $Fs \leq 1.60$. There was a significant difference between the Ext group and the CRF group, $F = 15.89$. The overall difference in the rats' levels of freezing to the consistent CS and the inconsistent CS was not statistically significant, $F = 2.69$, but there was a significant interaction between these two factors, $F = 6.13$. The source of the interaction between CS and group was identified by pairwise comparisons, which revealed that the Ext rats showed more freezing to the consistent CS than to the inconsistent CS, $F = 17.45$, whereas the CRF rats showed similar levels of freezing to the two CSs, $F < 1$. Finally, for all groups, there was a significant linear trend across presentations of the CS, $F = 81.44$, indicating extinction of responding within the test session, but this trend did not interact with any of the other contrasts, $Fs \leq 1.20$.

Discussion

This experiment confirmed the finding of Experiment 2: Rats show more responding to a CS when it is presented in its conditioning context than when it is presented in the context where another CS was conditioned. Further, this context specificity was only observed for rats whose fear of the CSs had been extinguished: We found no evidence for contextual control of responding among rats that had received continued pairing of the CSs with the US. The failure to observe context specificity among these rats indicates that exposure to the CSs per se is not sufficient for contextualization of the CS–US memory. Rather, it appears that the status of the CS–US association must be rendered ambiguous (such as occurs after extinction of the CS) for that memory to be under contextual control.

Experiment 4

Experiments 2 and 3 demonstrated that the expression of a CS–US association is controlled by the context where that association was learned but only for CSs that have been extinguished. This evidence is based on a comparison between rats for which both CSs had been extinguished versus rats for which neither CS had been extinguished. Thus, Experiments 2 and 3 show that extinction is necessary for the contextualization of the CS–US association. However, the specificity of this effect is yet to be determined. On the one hand, it is possible that rats that have undergone extinction training show context specificity for any CS, even a CS that has not been extinguished. For example, extinction may generally enhance the rats' processing of contextual cues, thus allowing them to display contextual specificity. On the other hand, the context specificity may reflect a change in the way rats process CSs once they have been extinguished, in which case context specificity would only be observed for extinguished CSs. This issue was examined in Experiment 4.

Two groups of rats were conditioned with CS A in Context A and CS B in Context B, before CS A was extinguished in a third context (C) for both groups. The rats were then tested for freezing to both CS A and CS B; each CS was tested either in the context where it had been conditioned (Group Consistent) or in the context where the other CS had been conditioned (Group Inconsistent). The test order was counterbalanced within each group. Thus, if extinction of a CS causes rats to show context specificity to all CSs, then we would expect to observe a difference between Groups Consistent and Inconsistent, as well as a difference between responding to the extinguished CS and the nonextinguished CS, but no interaction between these factors. In contrast, if rats only show context specificity for CSs that have been extinguished, then we should find such an interaction because the two groups should differ in their responding to the extinguished CS but should not differ in their responding to the nonextinguished CS.

Method

Subjects and apparatus. Thirty-two experimentally naïve male Wistar rats (*Rattus norvegicus*; 360–450 g) were obtained from the same source and housed in the same manner as in Experiment 1. The three sets of experimental chambers and two CSs were those used in Experiment 1.

Procedure. Rats were handled for 3 days and assigned to two weight-matched groups (*n* = 16). On Day 1, rats were conditioned to CS A and CS B in Contexts A and B, respectively. The shock intensity was set at 0.6 mA for 0.5 s, as in Experiment 2. On Days 2 and 3, CS A was extinguished: On each day, all rats were placed into Context C for 20 min where CS A was presented eight times without the shock US. On Day 4, the rats were tested. This consisted of placing rats into Context A or B, where one of the CSs was presented four times for 30 s. On Day 5, the rats were tested with the other CS in the other context. Thus, both groups were tested with the extinguished CS (CS A) and the nonextinguished CS (CS B), and the order of testing was counterbalanced. For one group (Group Consistent), each CS was presented in the context where it had been conditioned; for the other group (Group Inconsistent), each CS was presented in the context where the other CS had been conditioned. Rats were scored for freezing as in Experiment 1, and the data were analyzed by a MANOVA (O'Brien & Kaiser, 1985). This assessed the linear trend across CS presentations within a test, for the difference between the extinguished CS and the nonextinguished CS, for the difference between Group Consistent and Group Inconsistent, and for the interaction between them. As in Experiment 3, test order was included as a factor in the analysis.

Results

The level of freezing to the context prior to the presentation of the CS was low. The mean levels of freezing in the final 30 s before CS onset were: 11.25% and 13.75% for rats tested in the consistent context with the extinguished and nonextinguished CSs, respectively; and 10.0% and 8.8% for rats tested in the inconsistent context with the extinguished and nonextinguished CSs. There were no significant differences between groups nor between tests, and the interaction of these factors was not significant, *F*s < 1.

The mean percentage of freezing to each presentation of the CS on test for both groups is presented in Figure 4. Rats showed less freezing to the extinguished CS than to the nonextinguished CS. Further, rats tested with each CS in its consistent context showed more freezing than the rats tested in the inconsistent contexts. Finally, the difference between Groups Consistent and Inconsistent was greater for the extinguished CS than for the nonextinguished CS.

The statistical analysis confirmed these observations. There was a significant difference between the group tested in the consistent contexts and the group tested in the inconsistent contexts, $F = 8.77$, $F_{critical}(1, 26) = 4.2$. There was a significant difference in freezing to the extinguished CS versus the nonextinguished CS, $F = 21.41$. Importantly, there was a significant interaction between these two factors, $F = 4.60$. Finally, there was a significant overall linear trend across the CS presentations, $F = 157.22$, but this trend did not interact with any other comparison, *F*s < 1. The source of the interaction between CS and group was identified by pairwise comparisons, which revealed that the consistent
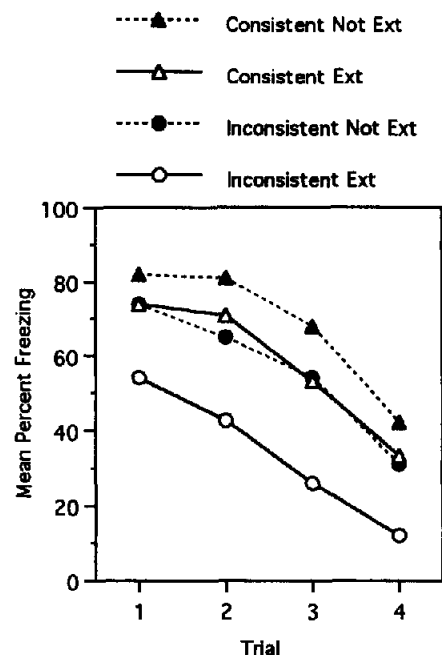
Figure 4. Mean percentage of time spent freezing to the conditioned stimuli (CSs) by rats in Experiment 4. Rats were exposed to pairing of two CSs with shock in separate contexts (A and B). One CS (extinguished [Ext]) was repeatedly presented without the shock in a third context (C). Rats were then tested for freezing across four presentations of each CS. For one group of rats (consistent), each CS was presented in the context where it had been conditioned; for the other group (inconsistent), each CS was presented in the context where the other had been conditioned.

and inconsistent rats differed significantly in their levels of freezing to the extinguished CS, $F = 11.73$, but they did not differ significantly when tested with the nonextinguished CS, $F = 3.01$.

Discussion

Experiment 4 confirmed that rats show differential responding to an extinguished CS depending on whether that CS is presented in its own conditioning context or in the context where another CS was conditioned. Further, this experiment has shown that if rats are trained with two CSs but only one is extinguished, then the contextual control over responding is specific to the extinguished CS. Thus, extinction training itself does not induce rats to contextualize their responding to any CS–US association; rather rats selectively contextualize their responding to extinguished CSs, without showing contextual control over nonextinguished CSs.

General Discussion

This series of experiments has demonstrated that rats use contextual information to regulate responding to CSs that have undergone extinction. Experiment 1 confirmed that rats show renewed responding to an extinguished CS if it is presented in a context different from that where it had been

extinguished. The difference in responding cannot be attributed to differences between the contexts in their excitatory or inhibitory association with the US, because neither context was associated with conditioning and both contexts were equally associated with extinction. The context specificity of extinction found in Experiment 1 indicates that rats remember the specific context where a CS has been extinguished, and rats use that information to control their retrieval of, or responding to, the CS–US association.

The present experiments have also demonstrated that rats' responding to a CS is controlled by the context where the CS was conditioned. In Experiments 2 to 4, rats were conditioned with two CSs, each in a different context, before one or both of the CSs were extinguished in a third context. We found that the rats responded more to the CS when it was presented in its own conditioning context than in the conditioning context of the other CS. This context specificity was only observed for CSs that had been extinguished: Responding to a CS was not affected by the context if the CS had not been extinguished. The absence of context specificity was not due to the relative unfamiliarity with the CSs among nonextinguished rats because there was no evidence for context specificity among rats that received repeated exposure to the CSs (matched in number and duration to the rats receiving extinction training) but for whom the CSs continued to be paired with the US. Moreover, if rats were conditioned with two CSs but only one was extinguished, the conditioning context regulated responding to the extinguished CS but not to the other CS. Thus, subjecting rats to an extinction treatment did not cause them to use the conditioning context to regulate their retrieval of all CS–US associations. Rather, the conditioning context only controlled retrieval of, or responding to, a CS–US association if that CS had been extinguished.

Following Rescorla's (1985) analysis of the control over responding exerted by inhibitors, there are at least four ways that the context might regulate responding to CSs: (a) by directly activating the US memory (Rescorla et al., 1985); (b) by influencing the response output (Wagner & Brandon, 1989); (c) by affecting how the CS is processed (Wagner, 1976, 1981); or (d) by controlling retrieval of the CS–US association (Bouton, 1993, 1994). The experimental designs used here were chosen specifically to control for any direct excitatory or inhibitory associations between the context and the US or between the context and the response. Therefore, the first two alternatives listed above can be discounted because they do not predict the specificity of control observed here.

The specificity with which the contexts influenced responding indicates that the locus of control must involve the CS: either the CSs processing (Alternative 3) or its association with the US (Alternative 4). The simpler account is that each context affected processing of its associated CS. Such a mechanism has been proposed by Wagner (1976, 1981), who argued that, as a CS becomes associated with a particular context, the context comes to reduce the ability of that CS to activate its own representation into the focus of working memory. This account can be invoked to explain context specificity of extinction as was observed in Experiment 1.

Repeated presentations of each CS in the absence of its associated US result in the development of inhibitory associations that serve to oppose the ability of each CS to excite conditioned performance. However, across these presentations, excitatory associations are also formed between each context and its associated CS. The consequence of these context–CS associations is that exposure to each context on test excites the representation of its corresponding CS into the periphery of working memory, which serves to reduce the ability of that CS, but not the other CS, to gain access to the focus of working memory. This difference in the processing of the two CSs would translate into a corresponding difference in the degree to which each CS could elicit freezing based on its net excitatory value. However, this account cannot explain the context-specific facilitation of responding observed in Experiments 2 to 4. In those experiments, the association between each conditioning context and its respective CS would have meant that processing of each CS in the focus of working memory should be greater in the inconsistent conditioning context than in the consistent conditioning context. Therefore, the rats should have shown less responding to the CSs tested in their consistent conditioning context than in the inconsistent context. This is the exact opposite to the result obtained.

The ability of the context to increase or reduce responding clearly depends on the history of the CS–US association in that context. In other words, the most likely mechanism is that the context acts on the CS–US association itself (Alternative 4 described above): The conditioning context promotes retrieval of that association whereas the extinction context inhibits it (Bouton, 1993, 1994; Bouton & Swartzentruber, 1986). This implies hierarchical control over CS–US associations, as has been discussed previously in the literature on occasion setting (Holland, 1983, 1985; Rescorla, 1985, 1991).

The context specificity of responding reported here is largely consistent with Bouton's (1993, 1994) description of how animals use contexts to regulate conditioned responding. Specifically, Bouton has argued that retrieval of a CS–US association is context independent, if that is the only association learned about the CS. However, if the status of a CS–US association is ambiguous because the animal has had contrasting experiences with the CS, then the animal uses contextual information to disambiguate these memories. For example, when a CS is extinguished, the animal has two conflicting memories about that CS: the initial memory that it signaled the US and the later memory that the CS was no longer associated with the US. According to Bouton, the animal resolves this ambiguity by linking its memory of the second association (in this case, extinction) to the context where it was learned. Thus, the rats retrieve the memory that the CS no longer signals the US when the CS is presented in the extinction context, but outside that context they retrieve the original CS–US memory. Consistent with Bouton's theory, we found that rats showed no contextual control over responding when the association with the US was the only thing learned about a CS. On the other hand, if the CS was extinguished, and thereby rendered ambiguous, the rats did show evidence for contextual regulation of the extinction

memory. However, under these circumstances, we also found that retrieval of the CS–US association was controlled by the conditioning context. Thus, when the meaning of a CS is rendered ambiguous by extinction, rats not only contextualized the extinction memory but they also contextualized the original excitatory CS–US memory.

The present finding that a CS must be extinguished before it comes under contextual control is similar to Bouton's (1984) demonstration that responding to an extinguished CS can be reinstated by presentation of the US in the test context but not elsewhere (see also Bouton & King, 1986). This reinstatement effect was specific to extinguished CSs because presentation of the US did not produce a context-specific facilitation of performance to CSs that had not been extinguished, even when the CSs were matched in terms of the level of responding they elicited. Our findings are also reminiscent of Rescorla's (1985) demonstration that a facilitator (i.e., a cue which signals that a CS–US association holds) only increases responding to a CS if that CS has had a mixed history of reinforcement (see also de Brugada, Garcia-Hoz, Bonardi, & Hall, 1995). For example, a cue trained as a facilitator with one CS transferred its control over responding to a different CS, but only after the second CS had been extinguished (Rescorla, 1985; Swartzentruber & Rescorla, 1994). The transfer of control across CSs described in these studies is clearly in contrast with the evidence for specificity of control obtained in our experiments. However, there is evidence for specificity in the control facilitators exert over responding to CSs (Holland, 1985). Further, because our experiments were designed to detect CS-specific control by contexts, we could not determine the extent to which that control transferred across CSs in a manner analogous to the transfer of facilitation reported by Rescorla (1985).

Nevertheless, Rescorla's (1985) demonstration that a CS must be extinguished for it to be subject to the influence of a facilitator is relevant to understanding how the conditioning context came to exert facilitatory control over responding after CS extinction. The contextual control observed in Experiments 2 to 4 may reflect a change in the way the rats processed the CS. More precisely, the CS may only have become susceptible to contextual control once it had been extinguished. Thus, contextual control over responding, whether it be inhibitory (as in Experiment 1) or facilitatory (as in Experiment 2 to 4), may not represent an explicit strategy that rats use to resolve ambiguity about the meaning of a CS (because this would require that they retrospectively recognize that the CS had signaled shock in the conditioning context). Rather, contextual control over responding may reflect an automatic change in the way a CS is processed if that CS has a mixed reinforcement history. In keeping with Rescorla's (1986a,1986b) suggestion that facilitation and inhibition are functional opposites, our results might indicate that a context (or cue) only functions as a facilitator of a CS–US association if some other context (or cue) functions as an inhibitor for that association.

This description of the conditions for contextual facilitation can be used to explain another feature of the present data. Experiments 2 to 4 revealed that rats respond more to a CS in its conditioning context than in a different context once the CS has been extinguished. However, in each of these experiments, rats failed to show any such context specificity to CSs that were extinguished during the test session. For example, in Experiment 2 there was clear evidence for extinction of responding across the eight presentations of the CS at test in the groups that had not been previously extinguished (see Figure 2). As a result of this extinction, one might expect that the rats being tested in the consistent context would eventually show more responding than the rats being tested in the inconsistent context. However, there was no such difference. This can be explained if it is assumed that extinction of a CS in its conditioning context extinguishes the facilitatory control that context would otherwise exert over the CS–US memory. Such extinction of control by discrete (noncontextual) facilitators has been reported by Rescorla (1986a). Alternatively, contextual facilitation of responding may not develop when a CS is extinguished in its conditioning context because this would require that the same contextual cues serve both inhibitory and facilitatory roles for the same CS.

Finally, it should be noted that the present results do not agree with previous findings reported by Hall and colleagues (Bonardi et al., 1990; Hall & Honey, 1989, 1990; Honey et al., 1990). These investigators have found evidence for context specificity of excitatory responding even in the absence of explicit nonreinforcement, a result which contrasts with the present observation that conditioned responding generalizes completely across contexts in the absence of extinction or preexposure (see also Bouton & King, 1983; Bouton & Peck, 1989; Grahame et al., 1990; Lovibond et al., 1984; Westbrook et al., 2000). In contrast with Bouton's model, Hall and Mondragón (1998) have argued that a CS does not need to be ambiguous for contextual control over that CS to be expressed. They suggested that instances where context specificity of responding has not been observed (e.g., the present experiments) may be due to the presence of context–CS associations that mask the context's own facilitatory control over the CS–US association. Specifically, during conditioning, animals learn the hierarchical relation between the conditioning context and the CS–US association, and as a result, the conditioning context facilitates responding to the CS. However, according to Hall and Mondragón, the facilitatory control exerted by the conditioning context can be masked by the expression of context–CS associations that were also learned during conditioning. As described earlier, when rats are tested in the consistent context, that context primes the memory of the CS into the periphery of working memory, thereby preventing the processing of the CS (when presented) in the focus of working memory, and thus reducing conditioned responding (Wagner, 1976, 1981). Thus, the context–CS association effectively counters the ability of the context to facilitate responding through hierarchical regulation of the CS–US association.

Hall and Mondragón suggested that arrangements, which promote context–CS associations (such as training with many CS–US pairings), reduce the opportunity to observe facilitatory control of responding by the conditioning con-

text. Consistent with this suggestion, Hall and Honey (1990) found that evidence for facilitatory control by the conditioning context was reduced when the number of CS–US pairings increased. On the face of it, this analysis cannot apply to our results because we exposed rats to only one CS–US pairing that should have maximized the chance of detecting context facilitation of responding, yet we failed to find any facilitation in the absence of extinction. However, our procedure may still have established strong context–CS associations because the contexts were novel at the time of conditioning (unlike Honey and Hall's experiment in which rats were extensively preexposed to the conditioning context which would have latently inhibited context–CS associations). Thus, we may have failed to observe facilitation of responding by the conditioning context in the absence of extinction because that facilitation was masked by the disruptive influence of context–CS associations.

The above analysis can be extended to explain our finding that the CS must be extinguished to reveal facilitatory control by the conditioning context. Specifically, presentation of the CSs in Context C may have served to extinguish the associations between Context A and CS A, and between Context B and CS B. This would have occurred if the associations between the contexts and CSs were bidirectional, as has been described for within-event associations between simultaneously presented stimuli (Rescorla & Durlach, 1981; Westbrook et al., 1995). Therefore, extinction of a CS in Context C would have disabled the conditioning context from priming the CS memory into the periphery of working memory on test, and thus unmasked the facilitation of responding produced by the conditioning context.

A further explanation of our results can be offered if one considers that the contexts used in these experiments were composed of multiple elements, some of which (e.g., the grid floor, the approximate size and shape of the chamber, the experience of isolation) were common to all contexts (we will refer to these as X elements), whereas other elements were unique to each context. The ability of Contexts A and B to facilitate responding to CS A and CS B, respectively, would be confined to the facilitatory control that accrues to the unique elements of those contexts, because the common X elements would facilitate responding to both CSs. In the absence of extinction in Context C, the contribution of the unique elements in A and B to facilitation of responding would be relatively small (especially because the X elements would have had twice as many CS–US pairings in their presence, and therefore twice the opportunity to acquire facilitatory control). However, extinction of the CSs in Context C could be expected to extinguish the facilitatory control of the X elements (Rescorla, 1986a). This would increase the relative contribution to responding exerted by the unique elements, thus increasing the likelihood of detecting differential responding in each context. In contrast, continued reinforcement of the CSs in Context C (as in Experiment 3) would have increased the facilitatory control acquired by the X elements, thus obscuring further any differential control exerted by the unique elements.

In conclusion, these experiments demonstrated contextual control over responding to an extinguished CS. Of importance, they have shown that animals do not just use contexts to retrieve memories for extinction, they also use contexts to retrieve excitatory CS–US memories. However, this latter contextual control is only observed for CSs that have been extinguished. Thus, our results could be interpreted to mean that animals use contextual information to retrieve a CS–US association, but only once that association has been rendered ambiguous, subjected to inhibitory modulation, or freed from the inhibitory influence of context–CS associations.

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